

WITHIN-BROOD VARIATION IN GROWTH AND CONDITION IN RELATION TO BROOD REDUCTION IN THE AMERICAN WHITE PELICAN

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ABSTRACT.—Loss of the second (B) chick in broods of American White Pelicans (*Pelecanus erythrorhynchos*) is common and has been attributed to starvation caused by sibling harassment. To examine this possibility in detail, we obtained weekly measurements of body weight and culmen length of individually marked A and B chicks from 80 nests sampled from seven subcolonies on three lakes in Manitoba, Canada, during the period when brood reduction normally occurs (first 2–3 weeks). Over half of the B chicks but none of the A chicks had bruises on the back or head. By the third measurement period, only 14% of the B chicks were alive, compared with 88% of the A chicks. Body size, weight, growth rates, and condition index (weight: culmen ratio) of the B chicks were all depressed relative to the A chicks. Evidence was obtained that B chicks succumbing within a given week weighed less and had smaller condition indices at the start of that week than did those that survived. Condition indices, which can be expected to reflect current food intake levels, exhibited greater within-brood disparity ($A > B$) for broods in which the B chick was about to die. Results are interpreted as supporting the hypothesis that socially induced food deprivation is causally linked to brood reduction in this species. Received 30 July 1986, accepted 28 Nov. 1986.

The American White Pelican (*Pelecanus erythrorhynchos*) characteristically produces a clutch of 2 eggs (Palmer 1962), but rarely fledges more than one young per brood in any given year (Johnson and Sloan 1978, Knopf 1979, Cash and Evans 1986). Brood reduction, which normally occurs during the first 3 weeks after hatching, has been attributed primarily to starvation resulting from harassment of the later hatched smaller chick by its older sibling (Johnson and Sloan 1978, Cash and Evans 1986). Extensive bruises on the head and back of the smaller sibling at many nests (Cash and Evans 1986) attest to the severity of sibling pecks. As a result of these interactions, the smaller sibling is usually driven towards the back of the nest, away from the parent's bill and food. Only the larger young receives food at most feedings (Johnson and Sloan 1978, Cash and Evans 1986). Correlated with this disparity in feeding is a difference in growth of the 2 chicks within a brood.

Despite the hypothesized role of socially induced starvation as a cause of mortality in young white pelicans, quantitative measurements of growth rates and condition indices (Owen and Cook 1977), which would presumably reflect differential food intake, have not been reported. Here we

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compare growth and condition within broods of pelicans over the period when brood reduction normally occurs.

METHODS

Pelicans were studied in 1984 at 3 breeding colonies, East Shoal Lake, Dog Lake, and Kawinaw Lake; all in the interlake region of south-central Manitoba, Canada (see O'Malley and Evans 1980 for map and further description of colonies). To determine the start of nesting activities and to obtain an estimate of hatch onset, colonies at East Shoal Lake were monitored, from shore, two to three times weekly during the period of colony occupation in April (Evans and Cash 1985). This procedure enabled us to delay entering the colonies until the onset of hatch, thereby keeping disturbance to a minimum. Colonies at East Shoal and Dog lakes were visited weekly thereafter, from 4 to 25 June. One final visit to East Shoal Lake was made on 9 July. Kawinaw Lake was visited only once, on 14 June.

White pelicans normally breed synchronously within subcolonies, with greater variation between subcolonies (Knopf 1979, O'Malley and Evans 1980). Subcolonies were therefore selected as sampling units. Each subcolony was chosen to provide a large sample of nests with two young, as near to their date of hatch as possible. To permit assessment of growth at successively later times during the normal breeding season, one new subcolony was selected during each of the first three weekly visits to East Shoal and Dog lakes. Three separate subcolonies were sampled during the single visit to Kawinaw Lake. Fifteen nests were sampled at each subcolony with the exception of one subcolony at Dog Lake, where only 5 nests containing two young were available when it was first visited.

Nests from which measurements were to be taken at East Shoal and Dog lakes were marked with a numbered wooden stake, and a small monel metal web tag (size #1, National Band and Tag Co., Newport, Kentucky) was placed on a foot web of each nestling to permit individual identification on subsequent visits. Measurements of chicks were taken at the time they were marked and again on two subsequent visits, for a total of three measurement dates per bird. During the single visit to Kawinaw Lake, the untagged young were measured once. At all locations, the presence or absence of bruises on the back or head of each young was noted during the first measurement period.

To measure body weight, an individual was slung, with a noose attached to both legs, beneath a pesola scale of appropriate size (minimum accuracy $\pm 5\%$). As an additional measure of size and growth, culmen length was measured with a ruler to the nearest mm. To permit comparison of body energy reserves in young of different sizes, a condition index (Owen and Cook 1977) was calculated by dividing the square of body weight by culmen length, the result being expressed as a dimensionless value.

The larger chick in each nest at the time of first measurement was designated the A chick, the smaller one the B chick. Because of hatching asynchrony within the brood, these designations normally reflect the true hatching order of the two young within a given nest (Cash and Evans 1986).

Average age of the young from each subcolony was estimated by back dating, using mean body weight of the A chick in each brood as the criterion. Mean body weight at hatching was taken as 110 g (determined from 9 laboratory-hatched young taken from their nest sites at or near the pipping stage). Mean weight gain per day was estimated from the growth rates of a group of 5 colony-reared young whose weight at the time of first measurement (90–120 g, mean = 109 g) was similar to the newly hatched young measured in the laboratory. These colony-reared young were then assumed to be in their first day when first measured. They gained 75 g/day over the first week, and 170 g/day during the second week. Weight gain in pelicans is not always a reliable indicator of chick age, due to variable growth rates that

reflect variable food intake (Schreiber 1976). In the present study, variability was minimized by restricting age estimates to the A chick in each brood, and by obtaining age estimates as soon after hatching as possible. Thus the ages given below are approximate, not necessarily exact.

Starting at about the third week of life, young white pelicans begin to leave their nests and form larger groups, or creches (Evans 1984). Due to increased mobility of older young and associated risks of colony disturbance at that time, measurements were discontinued prior to young reaching their asymptotic weights and probably prior to their reaching the inflection point on the growth curve (cf. Schreiber 1976). It was therefore not possible to analyze growth by means of conventional growth curves (the assumptions required for computing growth curves from single visits were not met, cf. Ricklefs and White 1975). To analyze growth, we determined mean growth per day for each young over a given weekly interval between two successive measurements. Differences in growth were assessed by analysis of variance (ANOVA) and, where appropriate, *t*-tests.

RESULTS

Eighty-eight percent of the 80 web-tagged A chicks survived at least until the third measurement period. Survival was significantly lower for the 80 B chicks in the same nests ($\chi^2 = 75.4$, $df = 1$, $P < 0.001$), with only 14% surviving over the same period. No evidence was obtained to suggest that differential loss of web tags rather than mortality accounted for the drop in numbers between weeks. Of the 160 young at marked nests, only 2 were found with perforated web but no tag.

In the 80 nests initially marked, both young survived up to the third measurement period (>2 weeks of age) at only 8 nests (10%). The B chick became larger than the A chick at one of these 8 nests. The B chick, rather than the A chick, survived to the third measurement period at 2 additional nests. Bruises on the head or back were noted on 69 of 125 B chicks (55.2%, includes data from Kawinaw Lake visit) at the time of first measurement. None of the A chicks had visible bruises at that time.

The pattern of growth was similar at all subcolonies (Fig. 1) (Table 1). To test for growth differences among subcolonies across age levels, the mean daily growth rates at 3 subcolonies having similarly aged young at the time of first measurement (subcolonies 2 and 3 on East Shoal Lake and subcolony 3 on Dog Lake) were compared for A chicks with 2-way ANOVA with repeated measures on one variable (successive weeks). The other variable was the three different subcolonies included in this analysis. Differences between subcolonies were not significant for either body weight ($F = 0.29$; $df = 2,36$; $P > 0.05$) or culmen length ($F = 0.36$; $df = 2,36$; $P > 0.05$). Interaction between age and subcolonies was significant only for body weight ($F = 6.06$; $df = 2,36$; $P < 0.01$). Age differences were significant for increases in both body weight ($F = 162.9$; $df = 1,36$; $P < 0.001$) and culmen length ($F = 4.28$; $df = 1,36$; $P < 0.05$), with older young growing faster in each case. Subsequent *t*-tests indicated that in-

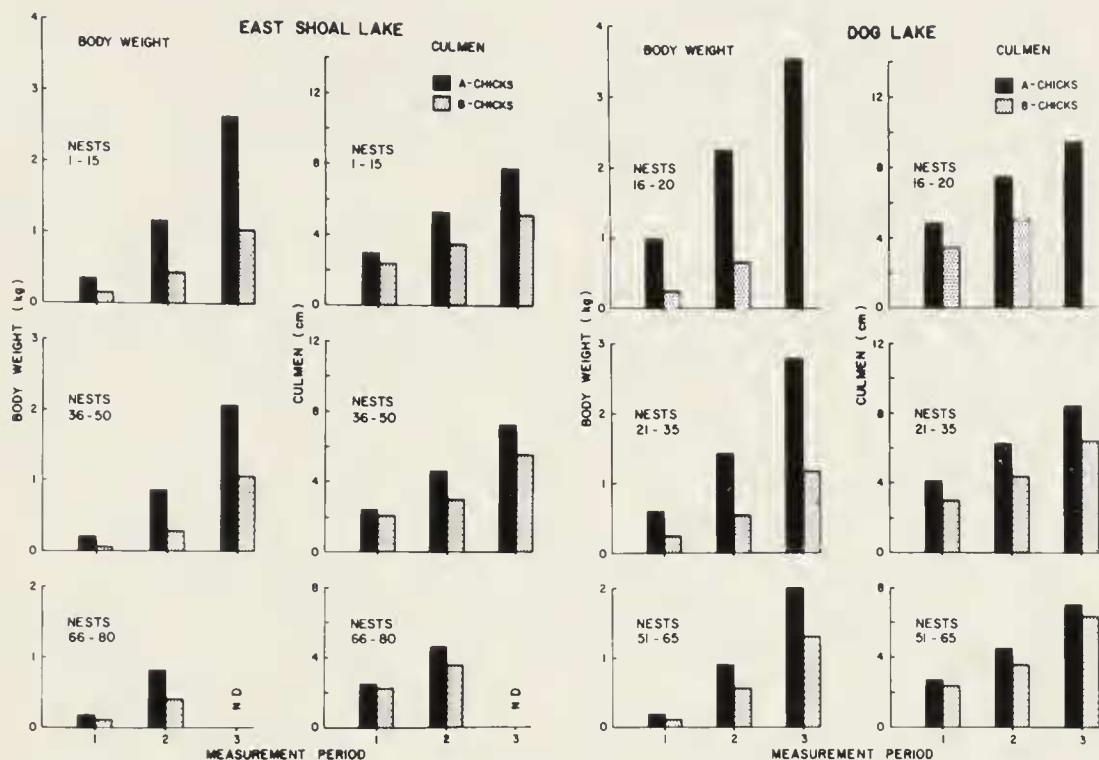


FIG. 1. Mean body weight and culmen length over three measurement periods for subcolonies at East Shoal Lake and Dog Lake. ND = not measured.

creasing growth rate with age was present for body weight at each of the three subcolonies included in the ANOVA and was also present ($P < 0.001$) at each of the remaining subcolonies that had been excluded from the ANOVA because they were older when first measured (Table 1).

Differences in growth with age were less consistent for culmen length. Only one of the three subcolonies included in the ANOVA showed significant age differences in growth rate ($t = 3.47, P < 0.01$). One of the subcolonies excluded from the ANOVA showed a significant effect of age ($t = 2.83, P < 0.02$), but the other did not ($P > 0.05$). Although there were some differences in growth rates between subcolonies, they were not sufficiently consistent to produce a significant main effect, and all subcolonies were combined for subsequent analyses.

For 9 B chicks that survived for all three measurement periods, mean daily increase in body weight was less during the first week than during the second week (51.0 vs 80.3 g/day), but the difference was not statistically significant ($t = 1.42, P > 0.05$). For culmen length, growth rate during the first week (1.9 mm/day) was significantly less than during the second week (2.7 mm/day: $t = 2.91, P < 0.02$).

Average growth rates suggest that the A chicks typically grew at a faster rate than did B chicks (Table 1). Direct comparison of A and B chicks present at 26 nests during both the first and second measurement periods

TABLE 1
 MEAN [\pm SD] GROWTH RATES FOR BODY WEIGHT AND CULMEN LENGTH OF YOUNG AMERICAN WHITE PELICANS AT SIX SUBCOLONIES IN 1984

Subcolonies	Date ^a	Age of chicks (days)	Number of chicks ^b		Weight (g/day)		Culmen (mm/day)	
			A	B	A	B	A	B
East Shoal								
1	4, 11 June	4, 11	11	5	117 \pm 36	33 \pm 19	3.2 \pm 0.4	1.3 \pm 0.1
	11, 18 June	11, 18	11	3	215 \pm 51	71 \pm 20	3.6 \pm 0.3	2.2 \pm 0.1
2	11, 18 June	2, 9	15	6	96 \pm 14	26 \pm 17	3.2 \pm 0.3	1.4 \pm 0.5
	18, 25 June	9, 16	15	3	171 \pm 25	94 \pm 3	3.6 \pm 0.5	3.1 \pm 0.6
3	18, 25 June	2, 9	14	9	88 \pm 25	34 \pm 20	3.2 \pm 0.8	1.9 \pm 0.7
	25 June	9, 23	14	ND ^c	169 \pm 31	ND	3.4 \pm 0.3	ND
	9 July							
Dog Lake								
1	4, 11 June	10, 17	5	1	178 \pm 32	33	3.7 \pm 0.8	1.3
	11, 18 June	17, 24	5	0	183 \pm 74		2.7 \pm 0.8	
2	5, 12 June	8, 15	15	6	121 \pm 35	40 \pm 44	3.1 \pm 0.5	1.9 \pm 0.9
	12, 18 June	15, 21	15	3	218 \pm 89	76 \pm 125	3.6 \pm 0.8	2.8 \pm 1.0
3	12, 18 June	2, 8	13	3	108 \pm 34	43 \pm 14	3.2 \pm 0.7	1.8 \pm 0.7
	18, 25 June	8, 15	10	0 ^d	152 \pm 37		3.4 \pm 0.3	

^a Growth rates calculated from measurements taken on the pairs of dates indicated.

^b Fifteen A and 15 B chicks were measured during the first visit at all subcolonies except at Dog Lake subcolony 1, where only 5 pairs were available. Number of chicks shown here represents number still alive and sampled on both of the indicated measurement dates.

^c ND = chicks inadvertently not measured.

^d One nest with a B but no A chick excluded from growth rate analyses. Measurements for this bird are included in Fig. 1.

indicated that the difference was statistically significant (body weight: $t = 11.04$, $P < 0.001$; culmen: $t = 9.24$, $P < 0.001$). Only 8 pairs of comparisons could be made between the second and third measurement periods due to mortality in the B chicks. Growth rates of the surviving B chicks at this age did not differ significantly from their sibling A chicks (body weight: $t = 2.16$, $P > 0.05$; culmen: $t = 1.54$, $P > 0.05$). Prior growth rates, between the first and second measurement period, for this same subsample of 8 nests followed the overall trend, in that growth of the B chicks was significantly less than the A chicks at that time (body weight: $t = 3.70$, $P < 0.01$; culmen: $t = 4.18$, $P < 0.01$). These results indicate that the initial disparity in growth rates between A and B chicks eventually becomes less severe at those nests where both chicks survive past the initial, and most intensive, period of brood reduction.

In the above analyses, body weight and culmen length tended to be similarly affected (Fig. 1), suggesting a strong correlation between these two measures. Inspection of young in the colony, however, suggested that the ratio of body weight to culmen length could be quite different among the young. In particular, B chicks appeared to be less plump, and often somewhat emaciated. This should result in a lower condition index, i.e., lower body weight relative to a linear measurement such as culmen length. For the first two measurement periods, condition indices were significantly less for the B chicks (Table 2). Mean values were not significantly less for the B chicks at the third measurement period, due primarily to a size reversal in one of the eight pairs measured at that time. Results for the single visit to Kawinaw Lake (Table 2) provided further evidence that condition indices of the A chicks were normally greater than those for the corresponding B chicks. Reduced indices for the smaller chicks (in all but one case the B chick) is consistent with the interpretation that the high mortality rates present in these young is related to reduced food intake.

If mortality in B chicks is causally related to loss of weight and starvation, then, of the B chicks alive in a given week, those that succumb during the immediately following week should show evidence of reduced growth compared with those B chicks that survive at least to the end of that week. Relevant measurements were obtained for 57 B chicks (Fig. 2). Those that succumbed between the first and second measurement periods (bars with diagonal lines) were less heavy and had smaller culmens when first measured than those that survived past the second period, but differences were not statistically significant (t -tests, $P > 0.05$). Differences at the time of the second measurement period were greater. B chicks that died between the second and third measurement period (open bars) were significantly lighter during the second measurement period than were those that survived past the third period ($t = 2.30$, $P < 0.05$). A similar,

TABLE 2
MEAN [\pm SD] CONDITION INDICES FOR A AND B CHICKS AT NESTS CONTAINING TWO
YOUNG WHEN MEASURED

Measurement period	No. pairs measured	A chick	B chick	<i>t</i>	<i>P</i>
1 ^a	80	0.57 \pm 0.07	0.48 \pm 0.06	10.81	<0.001
2	26	0.63 \pm 0.04	0.52 \pm 0.09	6.21	<0.001
3	8	0.61 \pm 0.05	0.55 \pm 0.03	1.91	0.1 >, >0.05
Kawinaw Lake	45	0.59 \pm 0.04	0.47 \pm 0.06	9.93	<0.001

^a See Table 1 for measurement periods for East Shoal and Dog lakes.

but not significant ($P > 0.05$), difference was present for culmen length. Although small sample sizes of B chicks surviving past the first measurement period preclude unequivocal conclusions, the results for older chicks suggest that a correlation exists between an individual's weight and its probability of survival.

If mortality in B chicks is related to weight loss and starvation, then condition indices should be less for those chicks that succumbed during a given week than for those that survived. The mean index value for 38 B chicks that perished before the second measurement period was 0.46, less, but not significantly so, than for the 19 B chicks that survived ($\bar{x} = 0.50$). For the 10 B chicks that succumbed between the second and third periods, the mean index value was 0.47 at the time of the second measurement period compared with 0.59 for the nine B chicks that survived past the third period ($t = 3.51$, $P < 0.001$).

Another relevant comparison is the difference in magnitude of condition indices between A and B siblings, a greater disparity within the brood being expected for broods in which the B chick is about to die. There was no significant difference ($P > 0.05$) in this value for young that succumbed between the first and second periods, but the effect was significant in broods where the B chick succumbed between the second and third measurement periods. For these older young, the mean difference in condition index values was 0.17 for the 10 broods in which the B chick did not survive until the next period, compared with only 0.05 for those broods in which the B chick did survive ($t = 3.36$, $P < 0.01$). In these older young there appeared to be a greater within brood disparity in food intake, as reflected in condition indices, for broods in which the loss of the B chick was imminent.

DISCUSSION

In agreement with several earlier studies (Behle 1958, Schaller 1964, Johnson and Sloan 1978, Knopf 1979, Cash and Evans 1986), brood

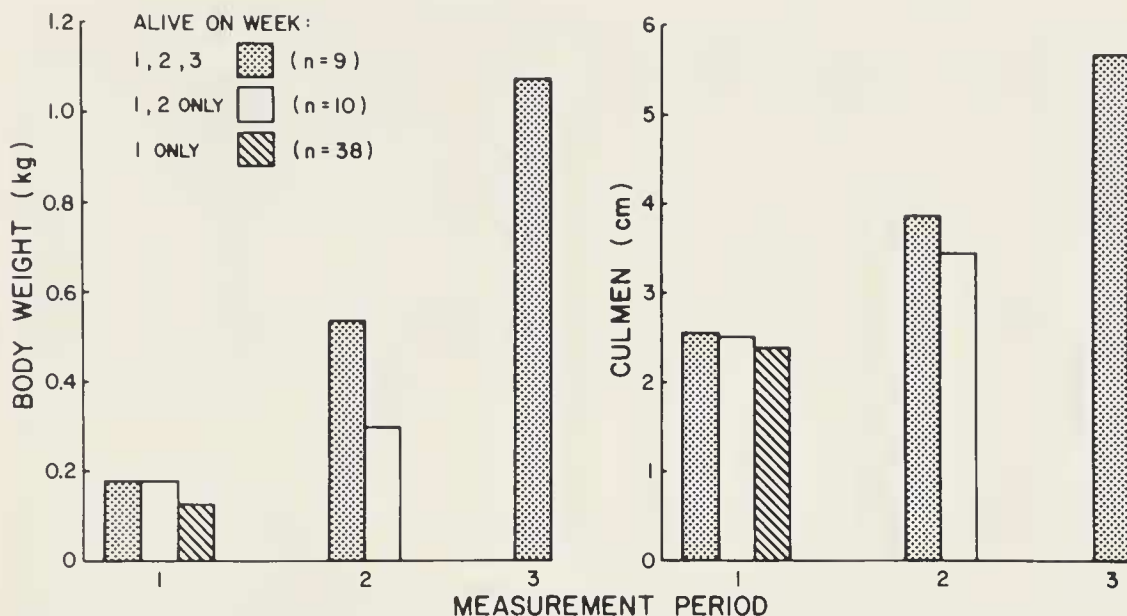


FIG. 2. Mean body weight and culmen length for B chicks that survived through measurement periods 1, 2, or 3.

reduction within the 80 marked nests sampled in this study was severe, with a maximum of 14% of B chicks surviving to the third measurement period (approximately 2 to 3 weeks of age). In contrast, survival of the A chicks over the same age was high (88%). Because mortality rates in this species tend to drop to low levels once the creche stage is reached at 2 to 3 weeks (Knopf 1979, Evans 1984), the results indicate that most breeding pairs fledged one young. This level of productivity is similar to that reported at East Shoal Lake in an earlier study (Cash and Evans 1986), but appreciably greater than reported in some other colonies (Johnson and Sloan 1978, Knopf 1979).

Mean growth rates for A chicks were similar among the subcolonies, and in most instances they exhibited a characteristic increase during the presumed exponential phase of the growth curve. A weekly increase in growth rates over the first three weeks has also been reported in the Brown Pelican (*P. occidentalis*) (Schreiber 1976). Relatively stable growth rates and high survivorship among the A chicks suggest that food supplies for the study populations were adequate for one-chick broods throughout the time of the study. Recent population increases in these and other colonies in this region (cf. Evans 1972, Evans and Cash 1985, Koonz and Rakowski 1985) support this conclusion. All of the populations in the study foraged extensively in one or both of two large lakes, Lake Winnipeg and Lake Manitoba, which evidently provided an adequate food supply at this time. Populations relying on smaller lakes for food may be subject to greater fluctuations in food availability and may experience greater fluctuations in reproductive output (Johnson and Sloan 1978).

The smaller size, significantly reduced growth rates, and smaller condition indices of the B chicks, combined with back or head bruises and high mortality rates in this group, all point to socially induced food limitation as a causative agent in brood reduction in this species. The tendency for B chicks that succumbed between the second and third measurement periods to be less heavy and have smaller condition indices than those B chicks that did not succumb during the same period provides further support for this interpretation. Also, most of the brood reduction in the marked sample of nests occurred between the first and second measurement periods, when growth rate differences between A and B chicks were most pronounced.

Between the second and third measurement periods, differences in growth rate between the A and B chicks did not reach statistical significance. Although the sample size was small for this comparison due to prior brood reduction, the results indicated that surviving B chicks did relatively better at obtaining food as they got older, provided they were able to survive the initial period of intense mortality. The similarity in condition indices within broods in which both young survived up to at least the third measurement period also suggests that the surviving B chicks were obtaining more food at that time. An increased ability of surviving older B chicks to obtain more food could account for instances (e.g., Knopf 1979) where both young fledge.

Although lack of food appears to be a strong correlate and probable causative agent in mortality of B chicks, starvation is not necessarily the immediate cause of mortality. As described elsewhere (Cash and Evans 1986), movement of the smaller chick to a more exposed position within or beyond the nest could result in death from exposure or from pecks delivered by neighboring adults. In some instances, the B chick is sufficiently harassed by its sibling that it is driven out of the nest, where it can fall prey to gulls (Evans 1984). In all of these instances, the action of food deprivation is presumably indirect, causing the chick to be more vulnerable to exposure, attack, or to being driven to a less safe location.

According to the interpretations of brood reduction developed by Lack (1954), selective mortality of the youngest sibling(s) is assumed to be due to an inability on the part of the parents to deliver sufficient food to the nest to feed all young adequately. Most evidence to date appears to support this interpretation (O'Connor 1978, Mock and Parker 1986, but see Clark and Wilson 1981 for a critique). In pelicans, it is also possible that parents are unable to deliver adequate amounts of food at the time brood reduction occurs, but direct evidence for this interpretation has yet to be produced. Direct evidence that parents are able to provide adequate food to the young nestlings is also lacking, but indirect support for this interpretation

comes from the timing of brood reduction which occurs during the first two weeks of age (Johnson and Sloan 1978; Cash and Evans 1986, this study), at a time when the young are still small (Fig. 1) and require relatively small amounts of food. Boluses of food observed being fed to older, creche-aged young typically are larger than the entire body size of the young at the time most brood reduction is occurring (Evans, pers. obs.). These considerations suggest that low levels of food intake by the B chick result mainly from behavioral causes, primarily the pecking and harassment by the A chick that causes the B chick to move towards the rear of the parent, combined with the tendency of the parent to passively feed whichever young is foremost in the nest (Cash and Evans 1986). Brood reduction at an early age in Blue-eyed Shags (*Phalacrocorax atriceps*) (Shaw 1985) has similarly been attributed to behavioral causes rather than to environmental limitations on food availability. In American White Pelicans, the presence of bruises on the head or back of over half of the B chicks but on none of the A chicks supports the conclusion that sibling harassment is prevalent and correlates strongly with lower growth and higher mortality in the B chicks.

To the extent that food limitation in B chicks results from dominance-related behavior between the siblings, initial size disparity can quickly accelerate as the smaller, underfed sibling becomes even less effective in aggressive interactions. This positive feedback arising from interactions among food, body size, and dominance status provides a plausible explanation for the rapidity with which B chicks can fall behind in overall growth, as well as for the rapidity with which brood reduction can occur.

Socially induced starvation within broods is rare in birds, but it is exhibited in other species in which brood reduction occurs well before the time that food might become limiting as the young grow larger (Shaw 1985, reviewed in Mock 1984). The possibility that white pelicans would normally be unable to feed both young throughout the creche stage when food demands become greater is also unproven, but the intense begging exhibited by single chick broods at that time (Cash and Evans, in press) suggests that food delivery by the parents to older young is not excessive. If so, elimination of a potential rival sibling at an early age would appear to be an adaptive strategy on the part of the dominant A chick, even though food may be abundant at the time brood reduction is effected.

In a recent study of brood reduction in Great Egrets (*Casmerodius albus*) and Great Blue Herons (*Ardea herodias*), Mock and Parker (1986) suggested that reproductive value, RV , of the youngest sibling(s) be divided into two components: that due to the production of an additional unit of reproductive success (RV_e ; i.e., in pelicans, both A and B chicks survive), and that due to replacement of the older sibling, the so-called insurance

option (RV_i ; i.e., in pelicans, the B chick survives at nests where the A chick dies). At the time of the final measurements in the present study, maximum possible RV_e for B chicks was 0.11, while maximum possible RV_i was only 0.03. Because there were still large differences in body size between the A chicks and remaining B chicks at the time of our last measurements (Fig. 1), further brood reduction could have occurred that would have reduced RV_e below the value of 0.11. In a previous study (Cash and Evans 1986) at one of the same colonies (East Shoal Lake), we found that only the B chick survived at 9 of 50 marked nests and that no nests produced more than one young. Calculations based on these figures give an RV_i of 0.18, and an RV_e of zero. Other studies (Johnson and Sloan 1978, Knopf 1979) provide no data with which to calculate RV_i values, but indicate that up to at least 10% of nests in some regions may produce two offspring. This would give an RV_e value of 0.10, similar to the maximum possible RV_e obtained in the present study. In general, the total RV of white pelican B chicks appears to be lower than for the youngest siblings in broods of herons or egrets (cf. Mock and Parker 1986).

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RAPTOR RESEARCH FOUNDATION MEETING

The Raptor Research Foundation is an organization whose purpose is to stimulate the dissemination of information concerning raptorial birds among interested persons worldwide and to promote a better public understanding and appreciation of the value of birds of prey. Towards this objective, we are holding our annual meeting on 28-31 October 1987 at Boise, Idaho. The meeting will feature a symposium on the migration of raptors in western North America. General paper and poster sessions will follow the symposium. The Conference Committee Chairperson is Rich Howard, U.S. Fish and Wildlife Service, 4696 Overland Rd., Rm. 576, Boise, Idaho 83705 (Phone number 208/334-1888).